STUDIES IN NEOTROPICAL PALEOBOTANY. IX. THE PLIOCENE COMMUNITIES OF PANAMA—ANGIOSPERMS (DICOTS)[1]

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ABSTRACT

Fifty-one fossil dicotyledonous pollen types and 27 unknowns are described from the Pliocene Gatun Formation of Panama. These are *Cymbopetalum*, *Ilex*, cf. *Aguiaria*, *Bernoullia*, *Ceiba*, *Pseudobombax*, *Bursera*, cf. *Bucida*, *Combretum/Terminalia*, Mutisieae type, cf. *Cionosicys*, Ericaceae (types 1, 2), *Alchornea*, cf. *Glycydendrum*, cf. *Jatropha*, cf. *Stillingia*, *Quercus*, *Alfaroa/Oreomunnea*, *Acacia*, *Crudia*, *Erythrina*, *Utricularia*, Loranthaceae (types 1, 2), Malpighiaceae (types 1, 2), *Hampea/Hibiscus*, Melastomataceae, *Cedrela*, *Guarea*, *Eugenia/Myrcia*, *Cabomba*, *Hauya*, *Rhizophora*, *Chomelia* type, *Cosmibuena*, *Faramea* (types 1, 2), *Posoqueria*, *Casimiroa*, *Allophylus*, *Cupania*, *Paullinia*, *Serjania*, cf. *Bumelia*, *Symplocos* (types 1, 2), *Mortoniodendron*, *Aegiphila*, and *Petrea*. Spores of the lycopods and ferns, and pollen of the gymnosperms and monocotyledenous angiosperms, have been described previously. Paleoecological and paleoenvironmental interpretations will be presented in a concluding paper.

This paper completes the systematic treatment of plant microfossils recovered from the Pliocene Gatun Formation of Panama. Introductory material and the systematics of other groups (ferns, gymnosperms, and monocots) are given in Graham (1991), new records of previously unreported taxa are provided in Graham (1990), and the geology of the pollen-bearing deposits is summarized in Graham et al. (1985). Fifty-one dicotyledonous pollen types, together with 27 unknowns, are recognized here. Thirty-one fern, gymnosperm, and monocot microfossils, and one Pyrrophyta (dinoflagellate), were previously reported, bringing the total number of taxa to 110. Numerical representations, and paleocommunity and paleoenvironmental reconstructions will be presented in a concluding paper.

MATERIALS AND METHODS

Extraction and processing techniques are described in Graham (1985). Slides are labeled according to core number, depth, and slide number (e.g., SL-103, 253′ [feet], 2). Location of the specimens on the slides is by England Slide Finder coordinates (e.g., ESF L-44). Details of interwall morphology (e.g., homogeneous; columellae just visible) are described as seen in median optical section with light microscopy at the magnification indicated (e.g., 400×). All materials are deposited in the palynology collections at Kent State University.

SYSTEMATICS

ANNONACEAE

Cymbopetalum (Figs. 1, 2). Oblate, amb circular; nonaperturate(?); psilate; tectate-perforate, tectal perforations large, circular to irregular in outline, constituting ca. 40–50% of grain surface, columellae conspicuous, ca. 15 μm long; 180 μm.

Cymbopetalum consists of 11 to 13 species of trees and shrubs distributed from Mexico to tropical South America, with three species in Panama: *C. brasiliense* (Vell.) Benth., *C. costaricense* (J. D. Smith) R. E. Fries, and *C. languipetalum* Schery. Pollen of the modern species has been studied by Walker (1971a, b, c, 1972). *Cymbopetalum* is known only from the Gatun assemblage.

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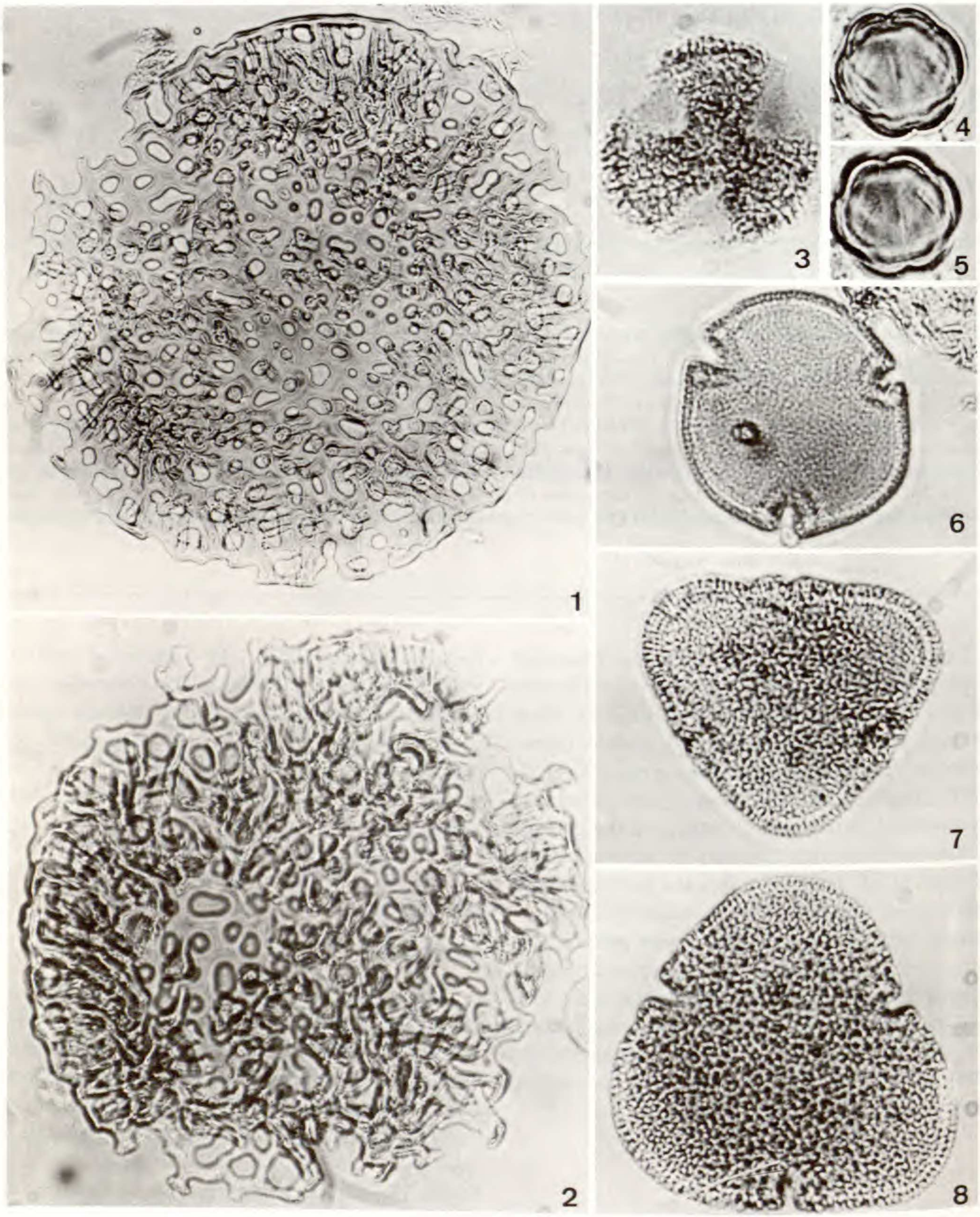


FIGURES 1–8. Fossil pollen from the Gatun Formation.—1, 2. *Cymbopetalum*, SL-103, 253′, 16, ESF N-26; SL-103, 253′, 9, ESF J-29.—3. *Ilex*, SL-103, 253′, 5, ESF E-18.—4, 5. *Combretum/Terminalia*, SL-103, 253′, 7, ESF D-18.—6. cf. *Aguiaria*, SL-103, 253′, 6, ESF 0-40.—7. *Bernoullia*, SL-103, 253′, 9, ESF G-21.—8. *Pseudobombax*, SL-103, 253′, 14, ESF P-44. All photographs taken at 400×; size in microns given in descriptions.

AQUIFOLIACEAE

Ilex (Fig. 3). Oblate-spheroidal, amb oval to circular, tricolporoidate (colpi occasionally obscured by sculpture elements), colpi meridionally elongated, equatorially arranged, equidistant, straight, 18–20 μm long, apices acute, inner margin frequently appearing undulate due to overlying sculpture elements, pore poorly defined, frequently obscure, situated at midpoint of colpus; intectate, clavate, wall 3–4 μm thick; 32–34 × 29–31 μm.

Ilex is widespread in northern Latin America, occurring in premontane to montane, wet to drier forest habitats.

Pollen of *Ilex* is found in low percentages in all of our Tertiary microfossil assemblages (Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, La Boca, and Paraje Solo formations). Other occurrences are summarized in Graham (1985, 1987).

BOMBACACEAE

cf. Aguiaria (Fig. 6). Oblate to peroblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, situated in interapical area, short (6–8 μm apex to equator), costae colpi 3–4 μm wide; finely reticulate (diameter of lumen 1 μm or less); tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 34–36 μm.

Pollen of the Bombacaceae is frequent in low percentages in Gulf/Caribbean Tertiary deposits. Assignment of some types to modern genera is difficult because of overlap with the Sterculiaceae and Tiliaceae, and the occurrence of several fossil forms that do not correspond to the pollen of any modern genus in our reference collection or in the literature (Graham, 1989: 59). The specimens are of the *Aguiaria* type (Tsukada, 1964, pl. VII, figs. 10–14; Nilsson & Robyns, 1986, figs. 7f, g), a monotypic genus of Brazil. Similar specimens are known from the La Boca Formation (Graham, 1989), and a smaller, poorly preserved one from the Uscari Formation (Graham, 1987).

Bernoullia (Fig. 7). Oblate to peroblate, amb triangular, apices rounded; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, situated in interapical area, short (6–8 μm apex to equator), costae colpi 4–5 μm wide; finely reticulate (diameter of lumen 1 μm or less), tectate-perforate, wall 3 μm thick, columellae evident in median section (400× magnification); 43–47 μm.

Bernoullia comprises three species of large, tropical trees distributed from Mexico to South America. The pollen specimens are similar to the pollen of *B. flammea* Oliver of Mexico and Central America. A specimen from the San Sebastian Formation (Graham & Jarzen, 1969, fig. 15) described as *Bernoullia* is different and probably is not *Bernoullia*.

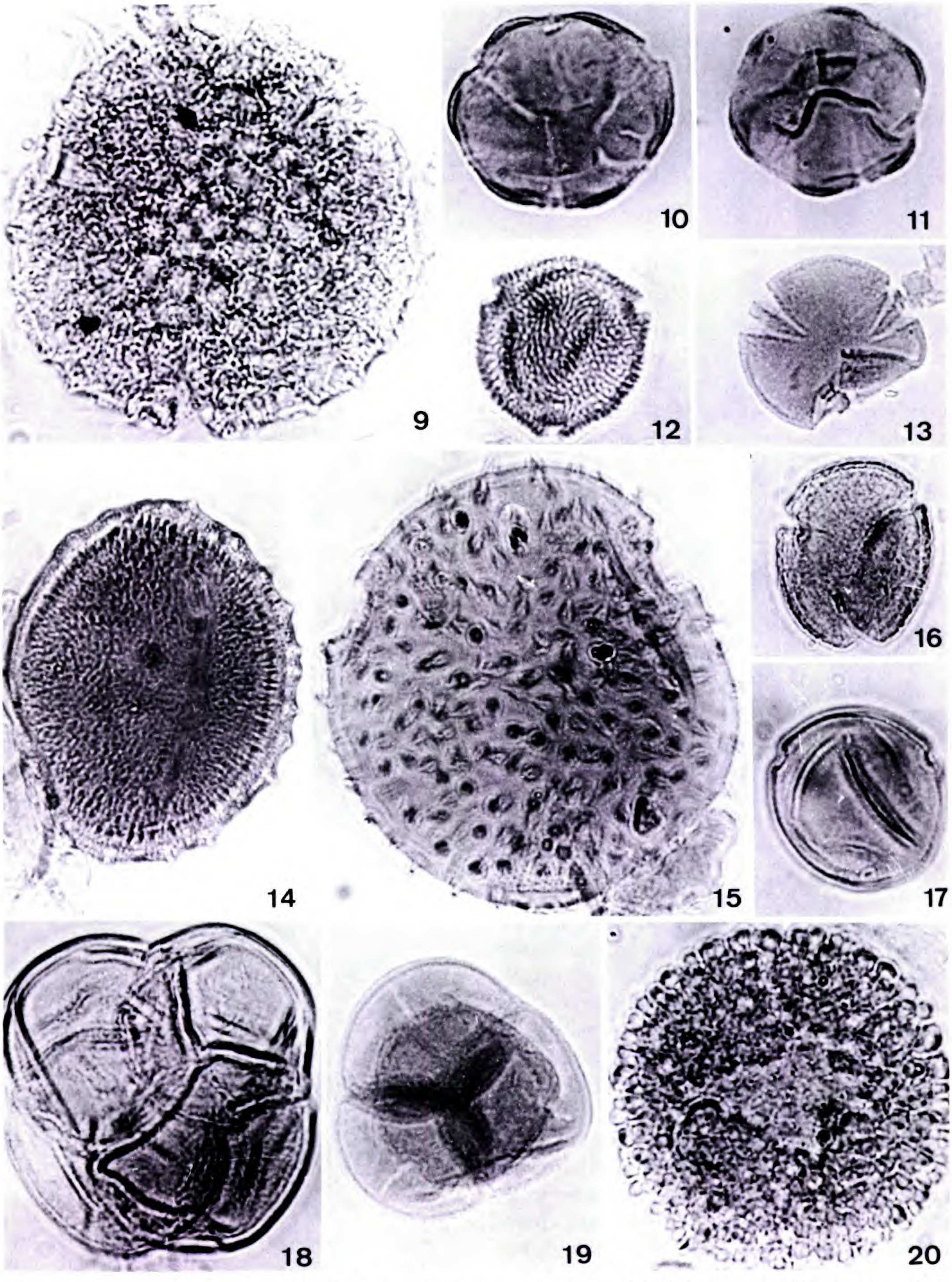
Ceiba (Fig. 9). Oblate to oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, short (12–15 μm apex to equator), costae colpi 4–5 μm wide; reticulate, muri narrow (1.5 μm), straight, smooth (appearing beaded from underlying columellae), lumina polygonal, varying in size, larger commonly in polar and mesocolpial areas and 6–8 μm diam., free sexine elements in lumina; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 68–74 μm.

The specimens are similar to pollen of *Ceiba pentandra* (L.) Gaertner, a large pantropical tree occurring in a wide variety of habitats. In Panama it commonly grows in the tropical moist and tropical dry forests, but also in other habitats. Microfossils are known from the La Boca Formation (Graham, 1989, fig. 34, as cf. *Ceiba*).

Pseudobombax (Fig. 8). Oblate to peroblate, amb triangular, apices rounded; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, situated in interapical area, straight, short (8–10 μm), costae colpi 5–6 μm wide; reticulate, muri smooth, narrow (1 μm or less), straight, lumina polygonal, diameter ca. 3 μm in polar area, diminishing to 1 μm or less at apices; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 54–58 μm.

In addition to difficulties noted earlier, the referral of Bombacaceae microfossils to certain modern genera is further complicated by nomenclatural changes among the extant taxa. In particular, *Bombax*, as treated in earlier taxonomic literature, included New World species. Herbarium material, pollen reference collections based on this material, and subsequent reports of microfossils from the Americas as *Bombax*, are frequent in the literature. Robyns (1964; Nilsson & Robyns, 1986: 6), however, placed species of *Bombax* in *Pseudobombax*, *Bombacopsis*, and other genera, with *Bombax* considered an Old World, primarily African, genus. The Gatun specimens are similar to pollen of such species as *Bombax ellipticum* HBK in our reference collection (*Barkley 17M103*, Mexico, TEX), now treated as *Pseudobombax ellipticum* (HBK) Dugand.

In Central America *Pseudobombax* is represented by *P. septenatum* (Jacq.) Dugand, distributed from Nicaragua to Brazil and Peru. In Panama it occurs typically in the tropical moist forest, but is also known from tropical wet, tropical dry, and premontane moist forests (Croat, 1978: 591). Similar pollen occurs in the San Sebastian (Graham & Jarzen, 1969, fig. 22, as *Bombax*), and the La Boca (Graham, 1989, fig. 35) formations.



FIGURES 9–20. Fossil pollen from the Gatun Formation.—9. *Ceiba*, SL-103, 253′, 8, ESF D-41.—10, 11. *Bucida*, SL-103, 253′, 6, ESF G-25; SL-103, 253′, 1. ESF M-39.—12. *Bursera*, SL-103, 253′, 6, ESF V-49.—13. *Alchornea*, SL-103, 253′, 1, ESF T-47.—14. Mutisieae type, SL-103, 253′, 14, ESF J-35.—15. cf. *Cionosicys*, SL-103, 253′, 4, ESF J-21.—16. *Quercus*, SL-103, 253′, 9, ESF L-47.—17. *Alfaroa/Oreomunnea*, SL-103, 253′, 9, ESF R-39.—18, 19. Ericaceae, SL-103, 253′, 5, ESF N-26; SL-103, 253′, 10, ESF K-45.—20. cf. *Jatropha*. SL-103, 253′, 1, ESF X-34.

BURSERACEAE

Bursera (Fig. 12). Oblate-spheroidal, amb oval-triangular to nearly circular; triporate, pores equatorially arranged, equidistant, circular to slightly elongated equatorially, 3–4 μm diam., faint costae pori; striato-reticulate; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 28–30 μm.

Modern pollen of the Mexican species of *Bursera* has been studied by Palacios Chávez (1984). The fossil specimens are similar to *B. simaruba* (L.) Sarg. et al., a tree or shrub of widespread distribution from southern Florida, through Mexico and the Antilles, to Colombia, Venezuela, and the Guianas. It is typical of the tropical moist forest, but also occurs in tropical wet, tropical dry, premontane moist, and premontane dry forests. *Bursera* pollen is known from the San Sebastian (Graham & Jarzen, 1969, fig. 23) and Paraje Solo (Graham, 1976, figs. 63, 64) formations.

COMBRETACEAE

cf. Bucida (Figs. 10, 11). Prolate-spheroidal, amb circular, lobate due to thinning of wall at apertures; tricolporate with three pseudocolpi, colpi equatorially arranged, meridionally elongated, equidistant, straight, ca. 15 μm long (apex to equator), colpus margin entire to slightly dentate, pseudocolpi similar, slightly shorter (ca. 12 μm apex to equator), pores circular, 3 μm diam., situated at midpoint of colpus; scabrate; tectate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 30 μm.

Bucida is a genus of four species distributed from southern Florida to Central America and the Antilles. One species, *B. buceras* L., is listed for Panama (D'Arcy, 1987), a small tree or shrub growing in wet forests and strand thickets at elevations from sea level to about 1,000 m. It has been reported as a megafossil from the Eocene Wilcox Formation of Kentucky (Berry, 1941) and from the Tertiary of the Dominican Republic (Berry, 1921); however, these megafossil records have not been reevaluated using modern methods of foliar architecture and cuticular anatomy. As a microfossil it is known only from the Gatun Formation. Similar scabrate, tricolporate grains with three pseudocolpi occur in several families of the Myrtales (Combretaceae, Lythraceae, Melastomataceae); hence, the provisional cf. identification.

Combretum/Terminalia (Figs. 4, 5). Prolate-spheroidal, amb circular, lobate in polar view; heterocolpate, colpi three, equatorially arranged, meridionally elongated, equidistant, straight, 8–10 μm long (apex to equator), colpus membrane faintly and minutely granular, margin entire to slightly diffuse, pores faint, situated at midpoint of colpus, 3–4 μm diam., pseudocolpi three, alternating with colpi, slightly shorter (6–8 μm); psilate; tectate, wall 3 μm thick, wall homogeneous (400× magnification); 18–24 μm.

Pollen of the Combretaceae was surveyed to determine the possibility of distinguishing between the common tropical trees *Combretum* and *Terminalia* (Graham, 1980). Pollen of the two genera could not be distinguished consistently, especially in the limited numbers encountered in the dispersed state, and the microfossils are referred to *Combretum/Terminalia*. *Combretum* is widespread in the New and Old World tropics, with about seven species in Panama. It commonly grows as a coastal or shore plant in tropical wet, tropical moist, premontane wet, and premontane moist forests. *Terminalia* is also widespread and is represented in Panama by about nine species, typically growing in tropical wet, tropical moist, premontane wet, and premontane moist forests. Microfossils are known from the Gatuncillo, Culebra, and Paraje Solo formations.

COMPOSITAE

Mutisieae type (Fig. 14). Prolate to prolate-spheroidal; tricol(por?)ate (pores obscure), colpi equatorially arranged, meridionally elongated, equidistant, ca. 45–48 μm long; echinate, echinae ca. 2 μm long, broad at base, tectate, wall 8–9 μm thick, individual columellae and two wall layers evident in median section (400× magnification), inner wall 4–5 μm thick, outer wall (including ca. 2-μm spines) 3–4 μm thick; 68 × 60 μm.

Among the pollen types surveyed in our reference collection and in the literature, this specimen most closely resembles *Mutisia*. However, this is a South American genus of high altitudes and/or arid habitats, and these conditions are not known to have existed in southern Central America during the Tertiary. Because the survey of modern genera of the Mutisieae is not complete, the specimen is provisionally referred only to the Mutisieae type of pollen.

CUCURBITACEAE

cf. Cionosicys (Fig. 15). Spherical, amb circular; triporate, pores equatorially arranged, equidistant, circular, large (12–15 μm), inner margin entire; surrounded by faint, granular costae pori 3 μm wide; echinate, echinae 3–4 μm long, broadening at base, surface between echinae faintly scabrate; tectate, wall thin (3 μm) in relation to size of grain, frequently folded, individual columellae just visible in median section (400× magnification); 88–94 μm.

The Cucurbitaceae are eurypalynous (Ayala-Nieto et al., 1988; Campos, 1962; Dieterle, 1976; Marticorena, 1963; Melhem, 1966), and although several genera have large, echinate pollen grains, many of these are periporate. The Gatun specimens are similar to the triporate pollen of *Cionosicys*, but differ in that the spines are not as robust, hence the cf. identification. *Cionosicys* is a Caribbean genus of three species with one [*C. macranthus* (Pittier) C. Jeffery] in Panama. The plant is a large vine growing in moist forests and open thickets, often along streams from Mexico to Panama (Wunderlin, 1978).

The Cucurbitaceae are poorly represented in the Gulf/Caribbean microfossil record. Probably because of their large, relatively fragile pollen produced in small amounts, and their entomophilous pollination. The oldest pollen record for the family is from the Oligocene of Cameroon (Muller, 1981: 39). The family has not been reported previously from the Gulf/Caribbean Tertiary, although some large ornate forms reported as unknowns (e.g., Fig. 85) may belong to the Cucurbitaceae. Bartlett & Barghoorn (1973) reported a different form as *Sechium edule*-type pollen from Quaternary deposits in Panama.

ERICACEAE

Type 1 (Fig. 18). Tetrahedral tetrad; individual grains spherical (compressed in tetrad), amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, inner margin entire, colpi shared (continuous across contact between grains); scabrate; tectate, wall 2 μm thick, homogeneous (400× magnification); individual grains 30–34 μm, tetrad ca. 50 μm.

Type 2 (Fig. 19). These grains are similar to type 1, but are smaller. The individual grains are 25–28 μm diam. and the tetrads are 35–40 μm.

The occurrence of Ericaceae pollen in Gulf/Caribbean Tertiary deposits has been discussed by Graham (1987: 1511). Briefly, the specimens cannot be identified to genus, but the larger grains fall within the range of variation of *Cavendishia*, a large genus of about 150 species of epiphytic and terrestrial shrubs distributed from southern Mexico through Central America into South America as far as Bolivia. About 30 species are recognized for Panama, where they are most common at moderate to higher altitudes. Ericaceae pollen has been reported previously from the Uscari Formation.

EUPHORBIACEAE

Alchornea (Fig. 13). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 10–12 μm long, extending within 5 μm of pole, inner margin entire, distinct operculum 3 μm wide; faintly scabrate; tectate, wall 2 μm thick, homogeneous to columellae occasionally just visible in median section (400× magnification); 26–30 μm.

Alchornea is widespread in the Neotropics, represented by about eight species in Panama. It grows in tropical moist, premontane wet, and premontane rainforests at altitudes from about 300 to 2,000 m. *Alchornea* is frequently present in low percentages in Gulf/Caribbean Tertiary microfossil floras (San Sebastian, Uscari, Culebra, Cucaracha, La Boca, and Paraje Solo formations).

cf. Glycydendrum (Figs. 21, 22). Oblate to oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 8–10 μm long, inner margin entire to minutely lobate; clavate, clavae fine, ca. 2 μm long; intectate, wall 2–3 μm thick; 42–45 μm.

Glycydendrum is one of the few genera presently confined to South America (Amazonian Brazil) that appears to be represented in southern Central American Tertiary deposits. Similar pollen occurs

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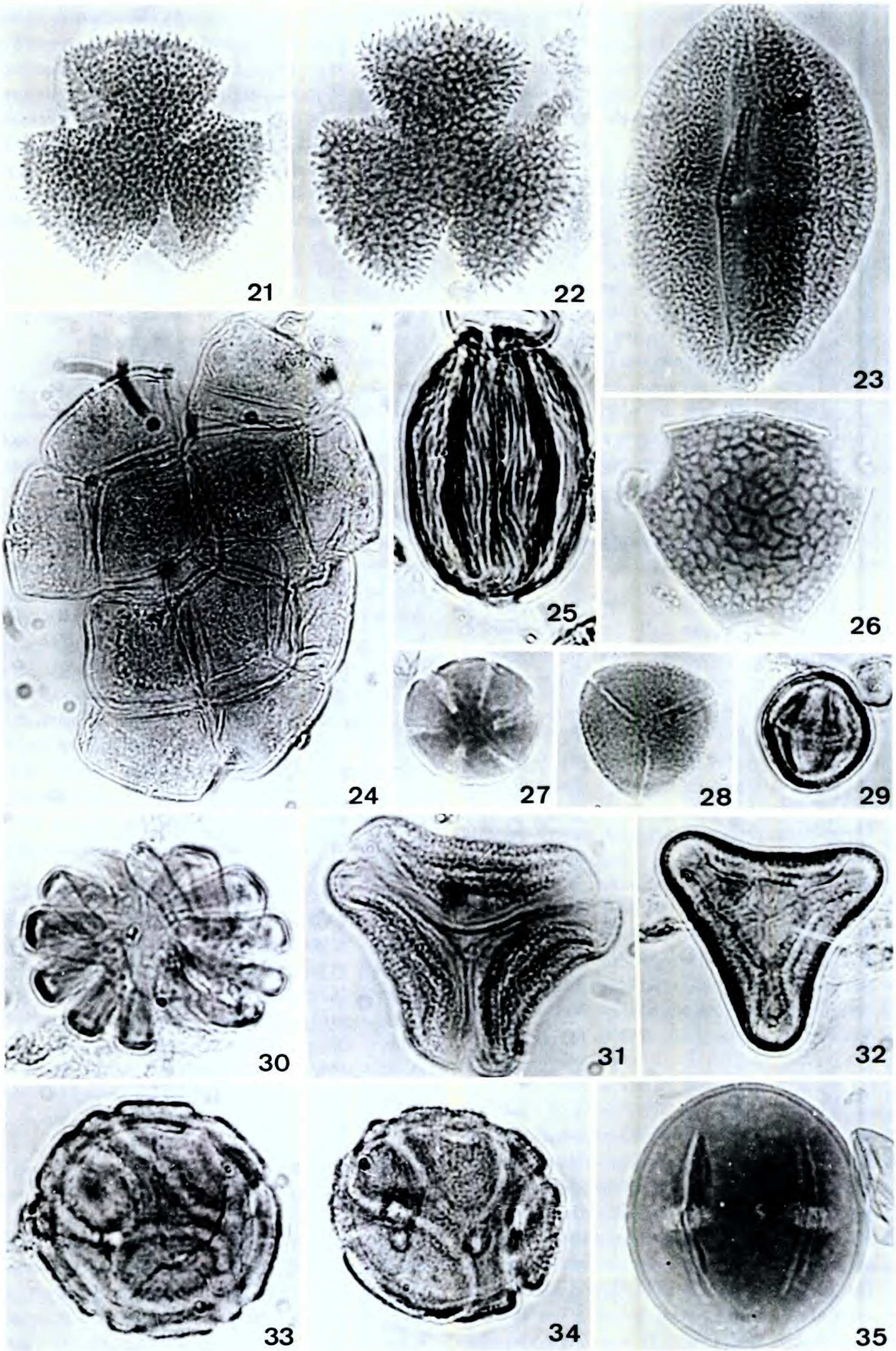
FIGURES 21–35. Fossil pollen from the Gatun Formation.—21, 22. *Glycydendrum*, SL-103, 253′, 8, ESF S-34; SL-103, 253′, 2, ESF K-22.—23. cf. *Stillingia*, SL-103, 253′, 14, ESF C-40.—24. *Acacia*, SL-103, 257′, 3, ESF K-27.—25. *Crudia*, SL-103, 253′, 11, ESF J-45.—26. *Erythrina*, SL-103, 253′, 4, ESF N-20.—27. Melastomataceae, SL-103, 253′, 2, ESF G-28.—28. *Eugenia/Myrcia*, SL-103, 253′, 1, ESF K-37.—29. *Rhizophora*, SL-103, 253′, 7, ESF E-14.—30. *Utricularia*, SL-103, 253′, 12, ESF M-31.—31. Loranthaceae type 1, SL-103, 253′, 8, ESF R-51.—32. Loranthaceae type 2, SL-103, 253′, 7, ESF D-33.—33. Malpighiaceae type 2, SL-103, 253′, 4, ESF V-24.—34. Malpighiaceae type 1, SL-103, 253′, 9, ESF J-21.—35. *Cedrela*, SL-103, 253′, 1, ESF F-52.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in *Tetrorchidium*, but the columellae in that genus are finer and nearly echinate. *Glycydendrum*-type pollen is present in the Uscari Formation, and Bartlett & Barghoorn (1973) reported *Glycydendrum* from Quaternary deposits in Gatun Lake, Panama.

cf. Jatropha (Fig. 20). Spherical, amb circular; nonaperturate; intectate, clavate, clavae relatively large and coarse, 3 × 4 μm, frequently triangular in outline; wall 4 μm thick; 56–60 μm.

The specimens have the wedge shape or triangular clavae typical of many Euphorbiaceae (e.g., *Croton, Manihot*), but these are not arranged into the stellate clusters or "crotonoid" pattern of these genera. The specimens cannot be identified below the level of family but are similar to pollen of *Jatropha*. The genus is widespread in Latin America, and four species are recorded for Panama. The plants range from the tropical moist forest to drier vegetation types. This type of Euphorbiaceae pollen has not been reported previously from Gulf/Caribbean Tertiary deposits.

cf. Stillingia (Fig. 23). Prolate, amb oval; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 59–62 μm long, inner margin entire, pore situated at midpoint of colpus, equatorially elongated, 2 × 4–5 μm; finely reticulate, lumina ca. 1 μm diam.; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 68–72 × 49–51 μm.

These large, prolate, triangular, reticulate grains are similar to *Stillingia*, a primarily New World tropical genus of 25–30 perennial herbs, shrubs, or small trees (Webster & Burch, 1967). The genus is represented in Panama by *S. zelayensis* (HBK) Muell.-Arg., which produces pollen similar to the Gatun specimens. *Stillingia* has been reported previously from the Paraje Solo Formation (as cf. *Stillingia*; Graham, 1976, fig. 114).

FAGACEAE

Quercus (Fig. 16). Prolate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 15–18 μm long, inner margin entire; scabrate; tectate, wall 2 μm thick, homogeneous; (400× magnification); 38 μm.

This is the earliest record of *Quercus* in Tertiary deposits of southern Central America, and it is rare in these Gatun sediments. It was more abundant in the Pliocene Paraje Solo Formation of Veracruz, Mexico, and first appeared in South America about 900,000 years ago (van der Hammen in Livingstone & van der Hammen, 1978). It was not recorded from Gatun Lake Quaternary deposits in Panama (Bartlett & Barghoorn, 1973), but was present in late Quaternary sediments from west coastal Costa Rica (Horn, 1985). Thus, the north-to-south migration of *Quercus* during the Tertiary and its relatively recent introduction into southern Central America and particularly South America (late Quaternary) seems clear, based on present data (Crepet & Nixon, 1989).

JUGLANDACEAE

Alfaroa/Oreomunnea (Fig. 17). Oblate, amb circular; triporate, pores equatorially arranged, equidistant, circular, 3–4 μm diam., inner margin entire; psilate to faintly scabrate; tectate, wall 2 μm thick, homogeneous (400× magnification); 27–30 μm.

Englehardia sensu lato was earlier considered a component of warm temperate vegetation in both the New and Old Worlds. Following the treatment of Stone & Broome (1975), however, *Englehardia* is now treated as an Old World genus, with related taxa in the New World assigned to *Alfaroa* and *Oreomunnea*. *Alfaroa* is a genus of about seven species growing in the highlands of Mexico, Central America, and northern Colombia. *Oreomunnea* comprises two species, "one ranging from the premontane cloud forests of southern Mexico to central Costa Rica (*O. mexicana* with two subspecies) and the other (*O. pterocarpa*) endemic to the Río Reventazón Valley of central Costa Rica" (Stone & Broome, 1975: 2).

Alfaroa/Oreomunnea-type pollen is known in the stratigraphic literature as *Momipites* and is present in the Gatuncillo, San Sebastian, Cucaracha, La Boca, and Paraje Solo formations. It is also reported from the Oligo–Miocene Simojovel Group of Chiapas, Mexico (Langenheim et al., 1967). The fossil record of the Juglandaceae, including *Alfaroa* and *Oreomunnea*, has been summarized by Manchester (1987).

LEGUMINOSAE

Mimosoideae

Acacia (Fig. 24). Sixteen-cell polyad; individual grains square to polygonal (compressed in polyad); nonaperturate, psilate to faintly scabrate; tectate, wall 2 μm thick, homogeneous to minute columellae just visible in median section (400× magnification); individual grains ca. 30 μm, polyad 120 × 88 μm (broken).

Twelve species of *Acacia* are found in Panama (fide Woodson & Schery, 1950), and five are listed for Barro Colorado Island (Croat, 1978). They are common in the tropical moist forest, but range into more open, drier habitats. *Acacia* pollen occurs in the San Sebastian, Culebra, and Paraje Solo formations.

Caesalpinioideae

Crudia (Fig. 25). Prolate; tricolporoidate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 30–35 μm long, extending nearly entire length of grain, pore area faint, circular, situated at midpoint of colpus; distinctly and coarsely striate, striae generally oriented parallel to long axis of grain, surface of striae psilate, margin entire, occasionally appearing beaded from underlying pores in foot layer/endexine; tectate but with occasional separation between sculpture elements, wall 2 μm thick, homogeneous (400× magnification); 44–48 × 28–32 μm.

Pollen of the Caesalpinioideae, including *Crudia*, has been studied by Graham & Barker (1981). *Crudia* is a South American, mainly Amazonian, genus of about 10 mostly riverine species. It is recorded in the stratigraphic literature as *Striatocolpites cataumbus* and in northern Latin America is known from the Gatuncillo, Cucaracha, and La Boca formations. Herendeen & Dilcher (1988) reported *Crudia*-type pods from the Eocene of western Tennessee.

Papilionoideae

Erythrina (Fig. 26). Oblate, amb oval-triangular; triporate, pores equatorially arranged, equidistant, circular (10–12 μm, compressed open), inner margin entire, surrounded by narrow margo ca. 4–5 μm wide formed by diminution of sculpture bordering pores; reticulate, muri thin (1 μm), low, smooth, sinuous, lumina polygonal, ca. 6–7 μm diam. in polar area, becoming finer toward equator and especially toward pores; tectate, wall 2–3 μm thick, homogeneous (400× magnification); 34–37 μm.

Pollen of the Erythrineae has been studied by Graham & Tomb (1974, 1977). This type of *Erythrina* pollen is produced by several Central American species, including *E. caribeae* Krukoff & Barneby, *E. castillejiflora* Krukoff & Barneby, *E. chiriquensis* Krukoff, *E. cobanensis* Krukoff & Barneby, *E. fusca* Loureiro, *E. guatemalensis* Krukoff, *E. williamsii* Krukoff & Barneby, and others. The plants occur through a wide range of habitats, including tropical wet, tropical moist, and premontane rainforests, from low to moderate elevations. *Erythrina fusca* sometimes forms pure stands in freshwater marshes (Holdridge, 1970 in Croat, 1978: 473).

LENTIBULARIACEAE

Utricularia (Fig. 30). Oblate-spheroidal, amb circular; stephanocolpate, colpi equatorially arranged, meridionally elongated, equidistant, ca. 15–18 μm long (apex to equator), 12 in number, inner margin entire; psilate; tectate, wall 2–3 μm thick, homogeneous (400× magnification); 42–45 μm.

Sixteen species of *Utricularia* are listed for Panama (D'Arcy, 1987), with two (*U. foliosa* L.; *U. obtusa* Sw.) occurring in the waters surrounding Barro Colorado Island. It is a freshwater, perennial, stoloniferous herb of widespread distribution from temperate to tropical regions in both the New and Old Worlds. Pollen has been reported from the Miocene of Senegal (Médus, 1975), and from the Pliocene Paraje Solo Formation of Mexico (Graham, 1976).

LORANTHACEAE

Type 1 (Fig. 31). Oblate, amb concavo-triangular, apices blunt; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 25–27 μm long (pole to apex), syncolpate, inner margin entire; mesocolpium baculate to slightly echinate, becoming psilate at apices; intectate in mesocolpium, tectate at apices, wall 1.5 μm thick, tectate portion homogeneous (400× magnification); 42–46 μm.

Type 2 (Fig. 32). Oblate, amb concavo-triangular, apices rounded; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 23–25 μm long (pole to equator), syncolpate, inner margin entire; finely striate with minute echinae between striae; tectate, wall 1.5 μm thick, homogeneous; 34–36 μm.

Both specimens are of the Loranthaceae type but cannot be referred to any one modern genus. Type 1 is generally similar to *Aetanthus*, and type 2 to *Psittacanthus*. Modern neotropical Loranthaceae pollen has been studied by Feuer & Kuijt (1979, 1980, 1985), and fossil pollen has been reported previously from the San Sebastian and Paraje Solo formations.

MALPIGHIACEAE

Type 1 (Fig. 34). Oblate-spheroidal, amb circular; periporate with colpal arcs connecting pores, pores circular, 4–6 μm diam., inner margin entire, inner margin of colpal arc minutely dentate, occasional free sexine elements on colpal membrane; scabrate; tectate, wall 3–4 μm thick, individual columellae evident in median section (400× magnification); 36–38 μm.

Type 2 (Fig. 33). Oblate-spheroidal, amb circular; periporate with colpal arcs connecting pores, pores circular, 3 μm diam., inner margin entire, inner margin of colpal arc minutely dentate, occasional free sexine elements on colpal membrane; scabrate, with occasional larger, low verrucae; tectate, wall 4–5 μm thick, homogeneous (400× magnification); 44–46 μm.

The Malpighiaceae are frequent in Gulf/Caribbean Tertiary deposits, but in low percentages. Although the family is moderately eurypalynous, most fossil pollen cannot be referred consistently to any one modern genus. Malpighiaceae pollen has been reported previously from the Gatuncillo, Uscari, Culebra, La Boca, and Paraje Solo formations.

MALVACEAE

Hampea/Hibiscus (Fig. 36). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., inner margin entire; echinate, echinae 5–7 μm long, occasionally curved, broad at base, surface between echinae scabrate; tectate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 75 μm (excluding spines).

There is sufficient overlap in the pollen of *Hampea* and *Hibiscus* that individual dispersed microfossils cannot be referred consistently to one genus. *Hampea* is represented in Panama by six species (D'Arcy, 1987), including the common *H. appendiculata* (J. D. Smith) Standley, which also occurs in Honduras and Costa Rica. It is a shrub to mid-size tree of tropical wet, tropical moist, premontane rain, and premontane moist forests. *Hibiscus* is represented by 12 species in Panama, including *H. sororius* L.f., a species common in marshy areas and coastal strand vegetation. Similar specimens have been recovered from the Culebra and Paraje Solo formations.

Melastomataceae (Fig. 27). Oblate-spheroidal, amb circular; heterocolpate, tricolporate with three pseudocolpi, colpi equatorially arranged, meridionally elongated, equidistant, straight, 6–7 μm long (apex to equator), inner margin entire, pores obscure, situated at midpoint of colpus, pseudocolpi slightly shorter to as long as colpi; psilate, tectate, wall 2 μm thick, homogeneous (400× magnification); 18–20 μm.

Dispersed fossil pollen of the Melastomataceae cannot be referred to any single modern genus, and in some cases they overlap morphologically with the pollen in other heterocolpate myrtalean families. The specimens serve only to record Melastomataceae-type pollen in Gulf/Caribbean Tertiary deposits. Similar pollen has been recovered from the Uscari and possibly the Culebra (unknown type 5) formations.

MELIACEAE

Cedrela (Fig. 35). Prolate-spheroidal; tetracolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 32–34 μm long, costae colpi 3–4 μm wide, pores situated at midpoint of colpus, slightly elongated equatorially, 4 × 6 μm; psilate; tectate, wall 3 μm thick, homogeneous (400× magnification); 50–52 × 42–44 μm.

The pollen of some species in Flacourtiaceae, Meliaceae, and Sapotaceae is similar and often difficult to separate in the dispersed fossil state. The relatively large (50 μm), tetracolporate specimens are most similar to *Cedrela* in our reference collection. Four species are listed for Panama (D'Arcy, 1987), and two are widespread in northern Latin America. *Cedrela odorata* L. occurs from northern Mexico to South America and the Antilles. In Panama it grows in tropical moist, tropical dry, and premontane wet forests. *Cedrela angustifolia* Sessé & Mociño occurs in the tropical moist and tropical dry forests and is most abundant along the Pacific slope. Both grow at low to moderate elevations. *Cedrela* has been reported previously from the Paraje Solo Formation.

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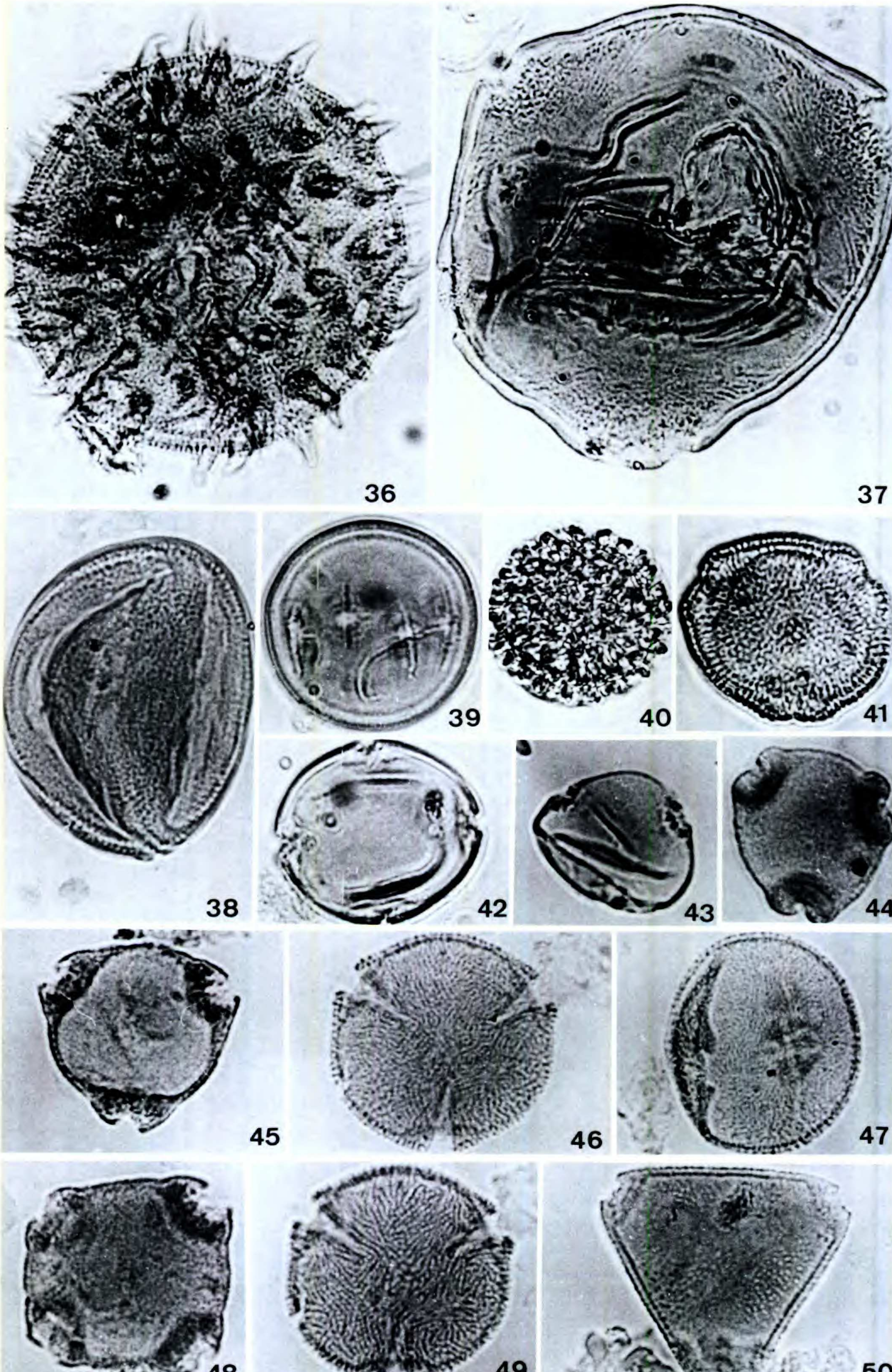
FIGURES 36–50. Fossil pollen from the Gatun Formation.—36. *Hampea/Hibiscus*, SL-103, 253′, 5, ESF N-37.—37. *Hauya*, SL-103, 253′, 14, ESF H-35.—38. *Cabomba*, SL-103, 253′, 1, ESF J-51.—39, 42. *Guarea*, SL-103, 253′, 13, ESF L-39; SL-103, 253′, 6, ESF S-29.—40. *Chomelia* type, SL-103, 253′, 7, ESF F-23.—41. *Faramea*, SL-103, 253′, 7, ESF D-34.—43. *Cosmibuena*, SL-103, 253′, 1, ESF M-44.—44, 45, 48. *Faramea*, SL-103, 253′, 1, ESF H-37; SL-103, 253′, 9, ESF H-20; SL-103, 253′, 2, ESF F-42.—46, 47, 49. *Casimiroa*, SL-103, 253′, 1, ESF P-40; SL-103, 253′, 1, ESF H-43.—50. *Paullinia*, SL-103, 253′, 7, ESF U-45.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Guarea (Figs. 39, 42). Oblate-spheroidal, amb circular, tetracolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, relatively short (12–14 μm), faint costae colpi 4–5 μm wide, inner colpus margin entire to minutely dentate, pores conspicuous relative to colpi, situated at midpoint of colpus, circular to slightly elongated equatorially, 6 μm diam., inner margin entire; psilate to faintly scabrate; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 36 × 39 μm.

Guarea is a large genus of about 150 species listed for the American tropics, with about 10 recorded for Panama that encompass a large number of synonymies (D'Arcy, 1987). Two common species in Panama are *G. glabra* Vahl and *G. multiflora* Adr. Juss., which range from Mexico to South America. In Panama these species occur in tropical wet and tropical moist forests at low to moderate elevations.

Guarea has been reported previously from the San Sebastian and Paraje Solo formations.

MYRTACEAE

Eugenia/Myrcia (Fig. 28). Oblate, amb triangular; tricolporate to tricolporoidate, syncolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 12–15 μm long, inner margin minutely dentate, pore obscure, situated at midpoint of colpus, ca. 1.5 μm diam.; scabrate; tectate, wall 2 μm thick, homogeneous (400× magnification); 24–28 μm.

The pollen of these genera cannot be distinguished consistently (Graham, 1980), and it is not possible to identify dispersed fossil pollen below the rank of family. The genera are widespread in Latin America and range through a variety of habitats. Similar pollen has been recovered from the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations.

NYMPHAEACEAE (CABOMBACEAE)

Cabomba (Fig. 38). Reniform; monosulcate, sulcus 45 μm long, bordered by faint, narrow (ca. 2 μm) margo; striate, striae appearing finely beaded due to underlying columellae; tectate, wall 2 μm thick, homogeneous (400× magnification); 58 × 34 μm.

Cabomba comprises six species of aquatic herbs in warm temperate to tropical regions of the New World. In Panama it is represented by *G. piauhyensis* Gardner, which has pollen similar to the Gatun specimen. Megafossils are known from the Paleocene Ft. Union Formation of North Dakota (see listings in LaMotte, 1952: 89). Microfossils are known presently only from the Gatun Formation.

ONAGRACEAE

Hauya (Fig. 37). Oblate, amb oval-triangular (aspidate); triporate, pores equatorially arranged, equidistant, large (10–12 μm diam.), slightly protruding, surrounded by conspicuous costae pori, elements of costae pori granular to elongated (striate), oriented parallel to equator; psilate to faintly scabrate; tectate, wall 3–4 μm thick, homogeneous (400× magnification); 102 μm.

Hauya comprises two species in Mexico and Central America: *H. heydeana* J. D. Smith (Chiapas, Mexico, and Guatemala) and *H. elegans* DC. (Hidalgo and Guerrero, Mexico to Costa Rica). It grows "with oaks and other lush middle elevation vegetation. It does not range upward into the pine belt or downward into the seasonally drier deciduous vegetation" (Graham & Jarzen, 1969, from Raven, pers. comm.). *Hauya* has been reported previously from the San Sebastian Formation.

RHIZOPHORACEAE

Rhizophora (Fig. 29). Prolate to prolate-spheroidal; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 12–15 μm long, inner margin entire, costae colpi 2–3 μm wide, pores situated at midpoint of colpus, elongated equatorially (costae transversalis), 1 × 4 μm; finely reticulate; tectate-perforate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 18–20 × 22–24 μm.

Rhizophora is not abundant in the Gatun samples. In the absence of other mangrove genera (e.g., *Pelliciera*), together with the diversity of upland and freshwater types, this suggests deposition in a swamp, shallow lake, or marsh only occasionally influenced by marine or brackish waters. Its geologic record in the Gulf/Caribbean region was summarized by Graham (1989). It is known from all our Tertiary formations in northern Latin America (Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, Culebra, La Boca, and Paraje Solo).

RUBIACEAE

Chomelia type (Fig. 40). Spherical, amb circular; nonaperturate (apertures obscure?); coarsely reticulate, muri 2 μm wide, straight, lumina polygonal, 2–8 μm diam.; tectate-perforate, wall 4–5 μm thick, individual columellae evident in median section (400× magnification); 28–34 μm.

This pollen type is common to several genera of the Rubiaceae (e.g., *Chomelia, Guettarda, Terebraria*) but is most similar to *Chomelia* in our reference collection. Nine species are listed for Panama (Dwyer, 1980; eleven in D'Arcy, 1987). The Panama species are trees, shrubs, or scandent shrubs growing in a variety of habitats, including swamp forests, tropical moist, and secondary forests. Similar pollen has been recovered from the Culebra, La Boca, and Paraje Solo formations [as the smaller *Terebraria* (22 μm); Graham, 1976, figs. 187–188].

Cosmibuena (Fig. 43). Oblate, amb circular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, oriented parallel to the equator (as observed in polar view), equidistant, 12 μm long, inner margin entire, pore situated at midpoint of colpus, circular, 3–4 μm diam., bordered by beaded annulus of fine, discontinuous ektexine elements; psilate; tectate, wall 2 μm thick, homogeneous (400× magnification); 28 μm.

The genus comprises about 12 species in Central and tropical South America, with two occurring in Panama: *C. ovalis* Standley, and *C. skinneri* (Oersted) Hemsley. The latter is most widespread, distributed from Mexico to Colombia and possibly Brazil. It is a component of tropical moist, premontane wet, and premontane rainforests. *Cosmibuena* is known only from the Gatun Formation.

Faramea type 1 (Fig. 41). Oblate, amb oval-triangular; triporate, pores equatorially arranged, equidistant, slightly protruding, 3–4 μm diam., annulus 3–4 μm wide, faint costae pori(?); finely reticulate, muri ca. 1 μm wide, lumina 1 μm or less in diameter; tectate-perforate, wall 4–5 μm thick; individual columellae evident in median section (400× magnification); 34–39 μm.

Faramea type 2 (Figs. 44, 45, 48). Oblate, amb oval-triangular; triporate, occasionally diporate or tetraporate, pores equatorially arranged, equidistant, circular to slightly oval, ca. 4 μm diam., inner margin entire to slightly dentate, surrounded by conspicuous annulus 5–6 μm wide; scabrate; tectate, wall 1.5 μm thick, wall homogeneous to individual columellae just visible in median section (400× magnification); 27–36 μm.

The pollen of *Faramea* is diverse, including diporate (e.g., Graham, 1985, figs. 64, 65) and tetraporate forms (Fig. 48), and is somewhat polymorphic with both thick-walled and thin-walled forms occurring on the same modern reference slide. Type 1 is similar to *F. talamancarum* Standley in our reference collection, and type 2 is similar to *F. occidentalis* (L.) A. Rich. *Faramea* is a large genus of about 125 species widespread in Latin America (Dwyer, 1980). Nineteen species are listed for Panama (D'Arcy, 1987), and these grow in a variety of habitats, including tropical wet, tropical moist, premontane wet, and premontane moist forests. Various pollen forms of *Faramea* have been recovered from the Gatuncillo, San Sebastian, and Paraje Solo formations.

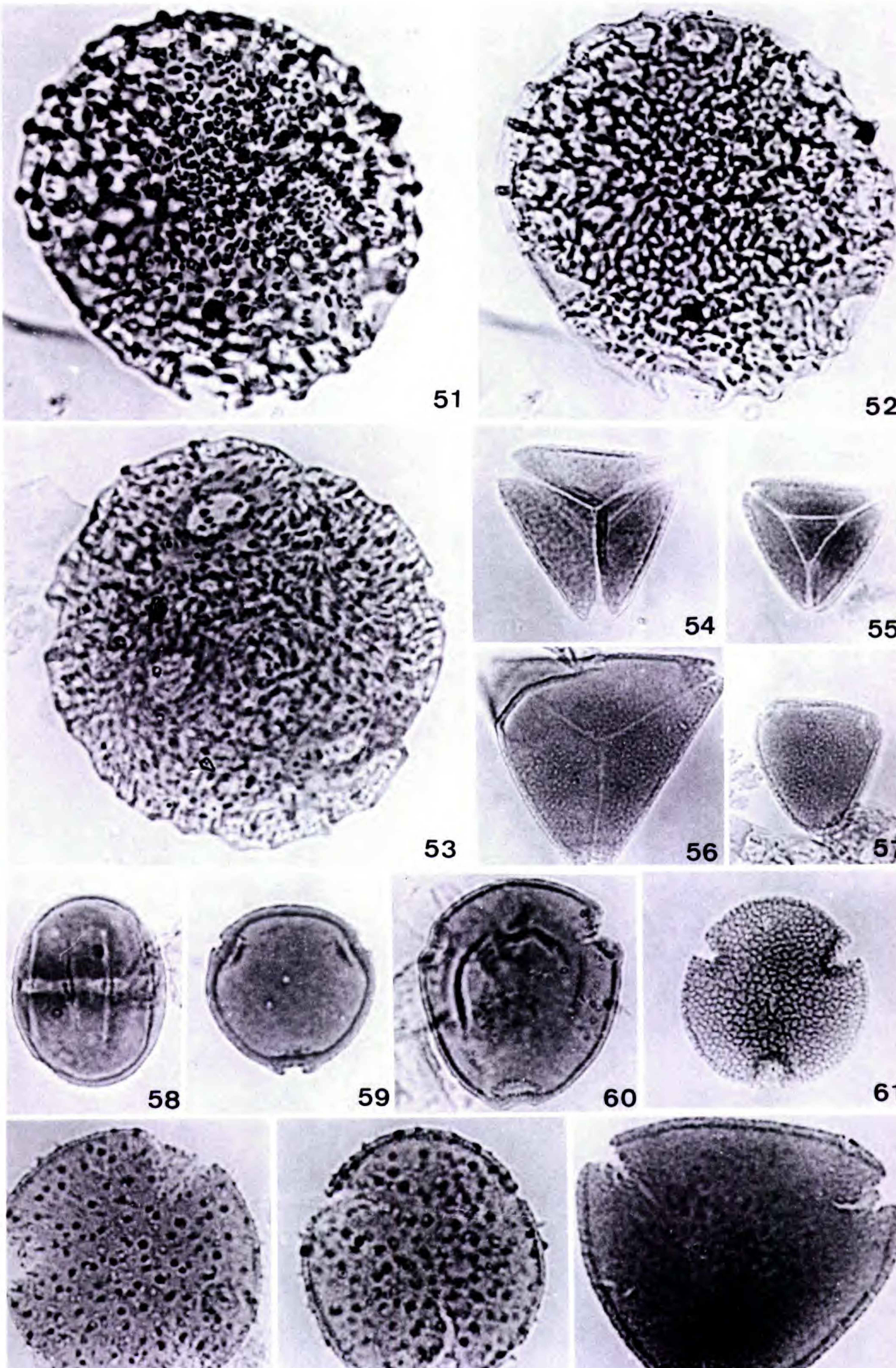
Posoqueria (Figs. 51–53). Spherical to oblate-spheroidal, amb circular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, short (12 μm apex to equator), broad at midpoint (9–12 μm), colpi faint and frequently obscure, pore circular, conspicuous (7–9 μm diam.), situated at midpoint of colpus, bordered by conspicuous annulus 4–5 μm wide; reticulate, reticulum irregular, lumen circular, 6–8 μm diam. in equatorial region, becoming finer and disrupted at poles, columellae supporting reticulum long (3–4 μm) clavae with smaller clavae-baculae occupying lumina of reticulum, muri smooth, slightly sinuous; tectate-perforate, wall 3–4 μm thick, individual columellae evident in median section (400× magnification); 68–70 μm.

Posoqueria includes about 15 species of trees and shrubs in Mexico, South America, and the Antilles. The most widespread species is *P. latifolia* (Rudge) Rose & Standley, growing primarily in the tropical moist forest, but also in tropical wet, premontane wet, premontane moist, and tropical dry forests. *Posoqueria* is known only from the Gatun assemblage.

RUTACEAE

Casimiroa (Figs. 46, 47, 49). Prolate-spheroidal, amb circular; tricolporate, equatorially arranged, colpi meridionally elongated, equidistant, 30 μm long, colpus margin entire to faintly dentate, costae colpi ca. 4–5 μm wide, pore situated at midpoint of colpus, equatorially elongated, 2 × 3 μm, bordered by costae pori 2 μm wide; finely striate-reticulate, arranged in swirl pattern, striae/muri occasionally appearing minutely beaded due to underlying columellae; tectate-perforate, wall 2 μm thick, columellae evident in median section; (400× magnification); 45–40 × 35–40 μm.

Six species of *Casimiroa* occur in Mexico and Central America, but none are listed for Panama (D'Arcy, 1987). Microfossils are known presently only from the Gatun Formation.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SAPINDACEAE

Allophylus (Fig. 57). Oblate to peroblate, amb triangular; triporate, pores equatorially arranged, equidistant, slightly elongated equatorially, 4 × 2 μm, faint costae pori; finely reticulate; tectate-perforate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 21–24 μm.

Allophylus is a large genus of about 190 species, with 13 listed for Panama (D'Arcy, 1987). The plants grow at low to moderate elevations in tropical wet, tropical moist, tropical dry, premontane wet, and premontane moist forests. Similar pollen has been reported from the Culebra and Paraje Solo formations.

Cupania (Figs. 54, 55). Oblate to peroblate, triangular; tricolporoidate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 10–12 μm long, syncolpate, apices of colpi occasionally branched to include triangular polar area; scabrate; tectate, wall 2–3 μm thick, homogeneous (400× magnification); 26 μm.

The pollen of *Cupania* is difficult to distinguish from *Matayba*. Those grains with a moderately thick wall, often including a triangular polar area, are most similar to *C. latifolia* HBK in our reference collection. Eleven species are listed for Panama (D'Arcy, 1987), and these grow primarily in tropical wet, tropical moist, and premontane moist forests. Similar grains are known from the Culebra and Paraje Solo formations.

Paullinia (Fig. 50). Oblate to peroblate, amb triangular; triporate, pores equatorially arranged, equidistant, 4–6 μm diam., costae pori ca. 4 μm wide; finely reticulate; tectate-perforate, wall 2–3 μm thick, individual columellae just visible in median section (400× magnification); 34–38 μm.

Paullinia is a large genus of about 194 neotropical species, with 49 species listed for Panama (D'Arcy, 1987). The plants typically grow in moist forests at low to moderate elevations. Similar pollen has been reported from the Gatuncillo and Paraje Solo formations.

Serjania (Fig. 56). Oblate to peroblate, amb triangular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 22–25 μm long, inner margin entire, syncolpate, pores situated at midpoint of colpus, 3–4 μm diam., faint costae pori; finely reticulate; tectate-perforate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 36–40 μm.

Twenty species of *Serjania* are recorded for Panama (D'Arcy, 1987), and these occur through a wide range of habitats at low to moderate elevations. Similar pollen has been reported from the Gatuncillo and Paraje Solo formations.

SAPOTACEAE

cf. Bumelia (Fig. 58). Prolate; tetracolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 18–21 μm long, inner margin entire to minutely dentate, costae colpi ca. 3 μm wide, pores situated at midpoint of colpus, elongated equatorially (colpi equatorialis), 2–3 × 4–5 μm, inner pore margin entire; psilate; tectate, wall 3 μm thick, homogeneous (400× magnification); 32–35 × 23–26 μm.

Pollen of tetra-aperturate Flacourtiaceae, Meliaceae, and Sapotaceae is difficult to distinguish consistently, especially in the dispersed fossil state. The Gatun specimens are most similar to *Bumelia* in our reference collection. *Bumelia* is a New World genus of about 23 species of trees and shrubs, ranging from the United States to Mexico, South America, and the Antilles (Blackwell, 1968). A single species, *B. persimilis* Hemsley, is listed for Panama (D'Arcy, 1987) and is distributed from Veracruz and Oaxaca, Mexico, to Venezuela. This pollen type was not reported previously in our Gulf/Caribbean assemblages.

SYMPLOCACEAE

Symplocos type 1 (Fig. 59). Oblate, amb oval-triangular to nearly circular; triporate (or tricolporate but with colpi short and obscure), pores equatorially arranged, equidistant, circular, 3 μm diam., annulus 3 μm wide; psilate to faintly sca-

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FIGURES 51–64. Fossil pollen from the Gatun Formation.—51–53. *Posqueria*, SL-103, 253′, 4, ESF P-19; SL-103, 253′, 8, ESF U-27.—54, 55. *Cupania*, SL-103, 253′, 8, ESF P-44; SL-103, 253′, 13, ESF J-42.—56. *Serjania*, SL-103, 253′, 15, ESF S-49.—57. *Allophylus*, SL-103, 253′, 2, ESF H-50.—58. cf. *Bumelia*, SL-103, 253′, 12, ESF T-47.—59. *Symplocos* type 1, SL-103, 178′, 2, ESF E-35.—60. *Symplocos* type 2, SL-103, 253′, 5, ESF V-33.—61. *Mortoniodendron*, SL-103, 253′, 13, ESF W-23.—62, 63. *Aegiphila*, SL-103, 253′, 12, ESF J-26; SL-103, 253′, 9, ESF T-48.—64. *Petrea*, SL-103, 255.5′, 5, ESF S-34.

brate; tectate, wall 3 μm thick, homogeneous (400× magnification); 28 μm.

Symplocos type 2 (Fig. 60). This specimen is similar to type 1 but is larger (38 μm). Type 1 is comparable to *S. chiriquensis* Pittier, and type 2 to *S. pychantha* Hemsley, in our reference collection.

Symplocos comprises about 350 species of trees and shrubs of pantropical distribution growing in a wide variety of habitats. Megafossils have been reported from the late Eocene Goshen Formation of Oregon (Chaney & Sanborn, 1933), and microfossils from the Maastrichtian of California (Chumura, 1973). It is known only from the Gatun Formation in the Tertiary of northern Latin America.

TILIACEAE

Mortoniodendron (Fig. 61). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–7 μm apex to equator), inner margin minutely dentate, costae colpi 4–5 μm wide; finely reticulate; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 34–38 μm.

The pollen of *Mortoniodendron* and its fossil record has been summarized by Graham (1979). The genus comprises about five species of small shrubs to tall trees growing from southern Mexico through Central America in tall moist forests at low to moderate elevations. Similar pollen has been recovered from the Gatuncillo and Paraje Solo formations.

VERBENACEAE

Aegiphila (Figs. 62, 63). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (9–12 μm apex to equator), inner colpus margin entire to slightly diffuse; echinate, echinae short (ca. 1 μm), moderately dense and uniformly distributed; tectate, wall ca. 1.5 μm thick, individual columellae just visible in median section (400× magnification); 45 μm.

Aegiphila comprises about 160 species of trees, shrubs, and lianas distributed from Mexico to South America (Brazil, Colombia, Venezuela, the Guianas, Peru). Twenty-one species are presently listed for Panama (D'Arcy, 1987), primarily in tropical wet, tropical moist, premontane wet, and premontane moist forests. The Gatun specimens are similar to *A. elata* Sw., a widespread species found along the margins of woods and streams. Fossil pollen of *Aegiphila* is known only from the Gatun Formation.

Petrea (Fig. 64). Oblate, amb oval-triangular, tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–8 μm apex to equator), margin entire to minutely dentate; scabrate; tectate, wall 3 μm thick, individual columellae just visible in median section (400× magnification); 52–56 μm.

There are about 30 species of *Petrea* distributed from northern Mexico to southern Brazil and the Antilles. Four species are known from Panama (D'Arcy, 1987), including the widespread *P. aspera* Turcz., which produces pollen similar to the specimens. Megafossils identified as *Petrea* have been reported from the late Eocene (now dated as earliest Oligocene) La Porte flora of California (Potbury, 1935). However, the holotype has an inflated, possibly cross-striated petiolule, which indicates that it is a legume (Doyle et al., 1988). Microfossils are known presently only from the Gatun assemblage.

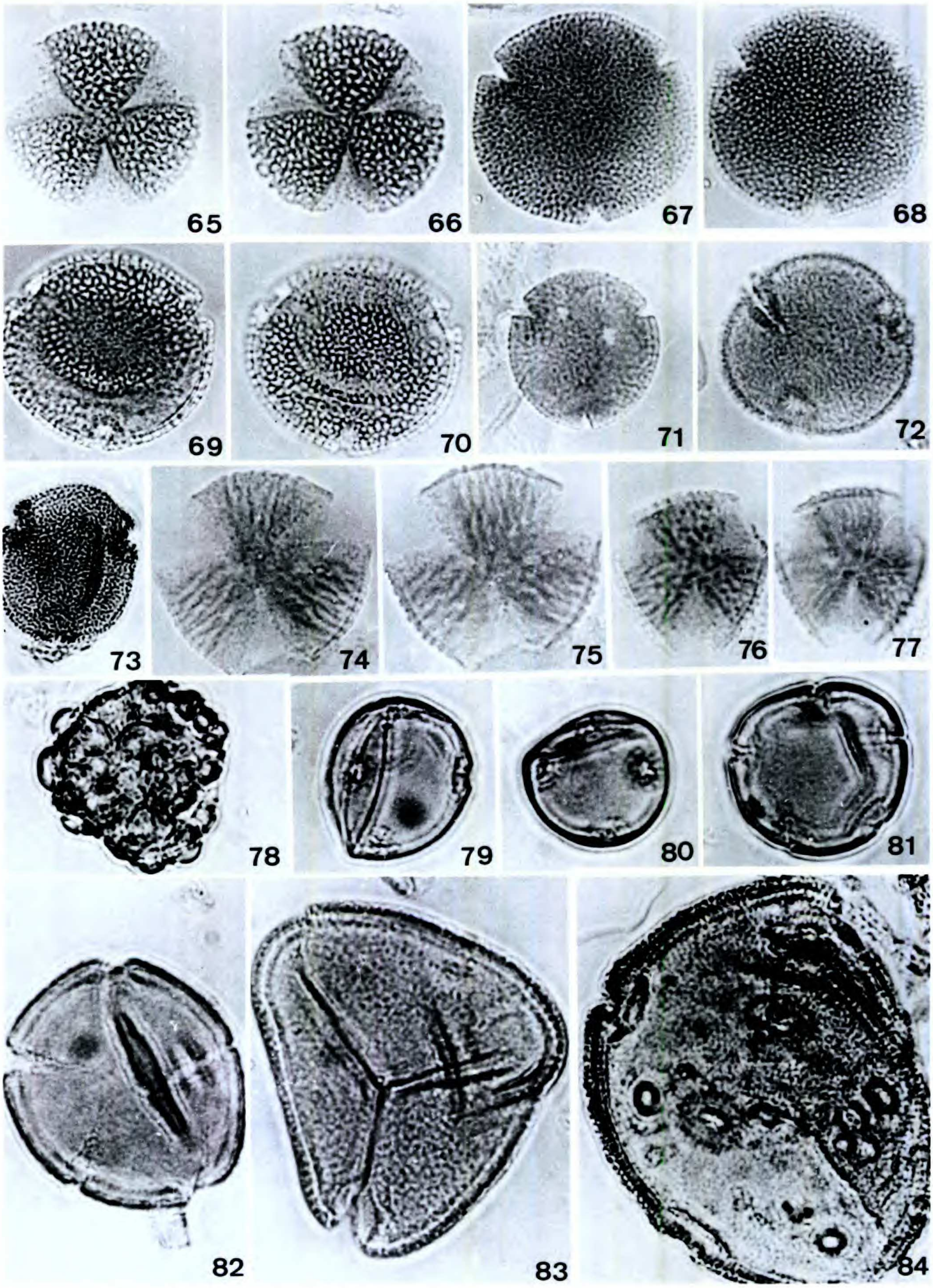
UNKNOWNS

In addition to the specimens identified from the Gatun Formation, a number of unknowns were recovered. Twenty-seven of the more common and/or distinctive ones are described below.

Unknown 1 (Figs. 65, 66). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 16–18 μm long (apex to equator), inner margin finely dentate; finely reticulate, width of muri 1 μm or less, diameter of lumina ca. 1.5 μm; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 35–40 μm.

These grains are similar to *Avicennia*, but all are oriented in polar view (*Avicennia* is prolate to prolate-spheroidal and is usually seen in equatorial view), and the wall is slightly thinner in the specimen.

Unknown 2 (Figs. 67, 68). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, short (3–4 μm apex to equator), inner margin finely dentate; finely reticulate, width of muri and diameter of lumina ca. 1 μm; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 35–39 μm.



FIGURES 65–84. Fossil pollen from the Gatun Formation.—65, 66. Unknown 1, SL-103, 253′, 1, ESF F-47.—67, 68. Unknown 2, SL-103, 253′, 1, ESF H-52.—69, 70. Unknown 3, SL-103, 253′, 7, ESF W-40.—71. Unknown 4, SL-103, 253′, ESF S-40.—72. Unknown 5, SL-103, 253′, 1, ESF P-37.—73. Unknown 6, SL-103, 257′, 1, ESF P-34.—74–77. Unknown 7, SL-103, 253′, 14, ESF Q-53; SL-103, 253′, 12, ESF M-40.—78. Unknown 8, SL-103, 253′, 15, ESF Q-41.—79, 80. Unknown 9, SL-103, 253′, 10, ESF J-42; SL-103, 253′, 13, ESF N-30.—81. Unknown 10, SL-103, 253′, 7, ESF T-27.—82. Unknown 11, SL-103, 253′, 5, ESF F-19.—83. Unknown 12, SL-103, 253′, 5, ESF O-14.—84. Unknown 13, SL-103, 253′, 7, ESF U-27.

Unknown 3 (Figs. 69, 70). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally arranged, equidistant, short (3 μm apex to equator), inner margin finely dentate; finely reticulate, width of muri and diameter of lumina ca. 1 μm; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 31–34 μm.

The wall of unknown 2 is slightly thinner and the columellae finer than in unknown 3. The short colpi and fine reticulum of these unknowns are suggestive of the Bombacaceae, but no exact match could be found among modern analogs in our reference collection.

Unknown 4 (Fig. 71). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (3–4 μm apex to equator); scabrate; tectate, wall 2 μm thick, columellae just visible in median section (400× magnification); 23–26 μm.

Unknown 5 (Fig. 72). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–7 μm apex to equator), costae colpi 3 μm wide; scabrate; tectate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 29–34 μm.

Unknown 6 (Fig. 73). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–7 μm apex to equator), costae colpi 4–5 μm wide; finely reticulate, width of muri and diameter of lumina ca. 1 μm; tectate-perforate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 32–35 μm.

Unknown 7 (Figs. 74–77). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, 12–15 μm long (apex to equator), broad (10–14 μm at equator, possibly compressed open), inner colpus margin diffuse; striate, striae coarse (3 μm wide), slightly sinuous, parallel and oriented at right angle to equatorial plane; tectate, wall 2 μm thick, homogeneous; 22–33 μm.

Unknown 8 (Fig. 78). Oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, colpi obscured by sculpture elements; verrucate, verrucae mound-like, translucent, variable in size, larger ca. 6 μm diam., base of verrucae and intervening surface area with small columellae giving granular appearance to portions of grain surface; tectate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 28–32 μm.

These grains are somewhat similar to *Elizabetha* (Leguminosae–Caesalpinioideae), but are smaller and have fine columellae giving a granular appearance to portions of the exine surface. They are also present in the La Boca (Graham, 1989, figs. 55, 56) and Paraje Solo (Graham, 1976, figs. 244, 245) formations.

Unknown 9 (Figs. 79, 80). Oblate-spheroidal to spherical, amb circular; tetraporate, pores equatorially arranged, equidistant, circular, 3 μm diam., annulus 3 μm wide, outer margin of annulus irregular and slightly granular; psilate; tectate, wall 2 μm thick, homogeneous (400× magnification); 22–25 μm.

These grains are very similar to *Cosmibuena* (Fig. 43) and may represent tetraporate forms of that genus. However, tetraporate grains have not been observed in our modern reference material of *Cosmibuena*, hence the designation of these specimens as unknown.

Unknown 10 (Fig. 81). Oblate, amb circular; stephano(5)colporate, colpi equatorially arranged, meridionally elongated, equidistant, short (ca. 5 μm), narrow (1 μm), inner margin minutely dentate, pores situated at midpoint of colpus, equatorially elongated, ca. 2 × 4 μm, costae pori; psilate; tectate, wall 2–3 μm thick, homogeneous (400× magnification); 31–33 μm.

Unknown 11 (Fig. 82). Oblate, amb circular; stephano(5)colporate, colpi equatorially arranged, meridionally elongated, equidistant, 15–18 μm long, tapering to prolonged acute apex, inner margin entire, pores situated at midpoint of colpus, 3 × 9 μm; scabrate to finely verrucate, scabrae/verrucae low, larger ca. 5 μm diam.; tectate, wall 4–5 μm diam., homogeneous (400× magnification); 45 μm.

Unknown 12 (Fig. 83). Oblate, amb triangular, apices rounded; trilete or trichotomosulcate, individual arms straight, ca. 30 μm long, extending to or nearly to margin, inner margin entire; scabrate/punctate, punctae (or spaces between scabrae) narrow, elongated, sinuous, becoming finely reticulate bordering apertures; tectate to tectate-perforate, wall 3 μm thick, individual columellae/punctae evident in median optical section (400× magnification); 60 μm.

This specimen may represent a trilete fern spore, but the wall structure suggests a trichotomosulcate palm pollen.

Unknown 13 (Fig. 84). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., evenly distributed, inner margin entire, costae pori 4–5 μm wide; scabrate; tectate, wall 4 μm thick, individual columellae evident in median section (400× magnification); ca. 75 μm.

Unknown 14 (Fig. 85). Spherical, amb circular; nonaperturate; echinate, echinae short (2–3 μm), somewhat variable in shape, mostly broad at base, moderately densely arranged, distance between echinae 1–3 μm; tectate, wall 2 μm thick, homogeneous (400× magnification); 75–80 μm.

The size and ornamentation of this grain suggest Cucurbitaceae, but an exact match could not be found. Some of the several folds simulate a trilete mark, but the specimen is provisionally interpreted as nonaperturate.

Unknown 15 (Fig. 86). Oblate, amb circular; stephano(6)colpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 20–22 μm long, inner margin minutely dentate; reticulate, muri narrow (1 μm or less), sinuous, lumina polygonal, ca. 3 μm diam., slightly smaller at poles; tectate-perforate, wall 3 μm thick, individual columellae (appearing as slight clavae) evident in median section (400× magnification), ca. 1 μm wide, spaced ca. 2 μm; 70–75 μm.

The specimen is similar to some Labiatae (e.g., *Hyptis*), but an exact match could not be found.

Unknown 16 (Fig. 92). Spherical, amb circular; nonaperturate; echinate, echinae 3–5 μm long, uniform width (2 μm) for most of length, then tapering abruptly near apex, occasionally curved; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 58 μm (excluding spines).

An irregular fissure extending nearly the entire length of the grain may represent a sulcus, but the margins are irregular, suggesting a split in the exine, and the specimen is interpreted provisionally as nonaperturate.

Unknown 17 (Fig. 91). Spherical, amb circular; nonaperturate; echinate, echinae 7–9 μm long, 3 μm wide at base, occasionally curved, more or less widely spaced (distance between echinae 6–10 μm), surface between spines scabrate; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 52 μm (excluding spines).

Unknown 18 (Figs. 87, 88). Oblate, amb circular; nonaperturate; reticulate, reticulum more or less obscure, shallow, muri narrow, sinuous, lumina polygonal; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 60 μm.

Unknown 19 (Figs. 97, 98). Oblate, amb circular; tricolpate (?, apertures obscure), colpi equatorially arranged, meridionally elongated, equidistant; reticulate, reticulum shallow (supporting columellae short, ca. 1.5 μm), muri narrow (1 μm or less), sinuous, lumina polygonal, larger lumina 3–5 μm diam.; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 65 μm.

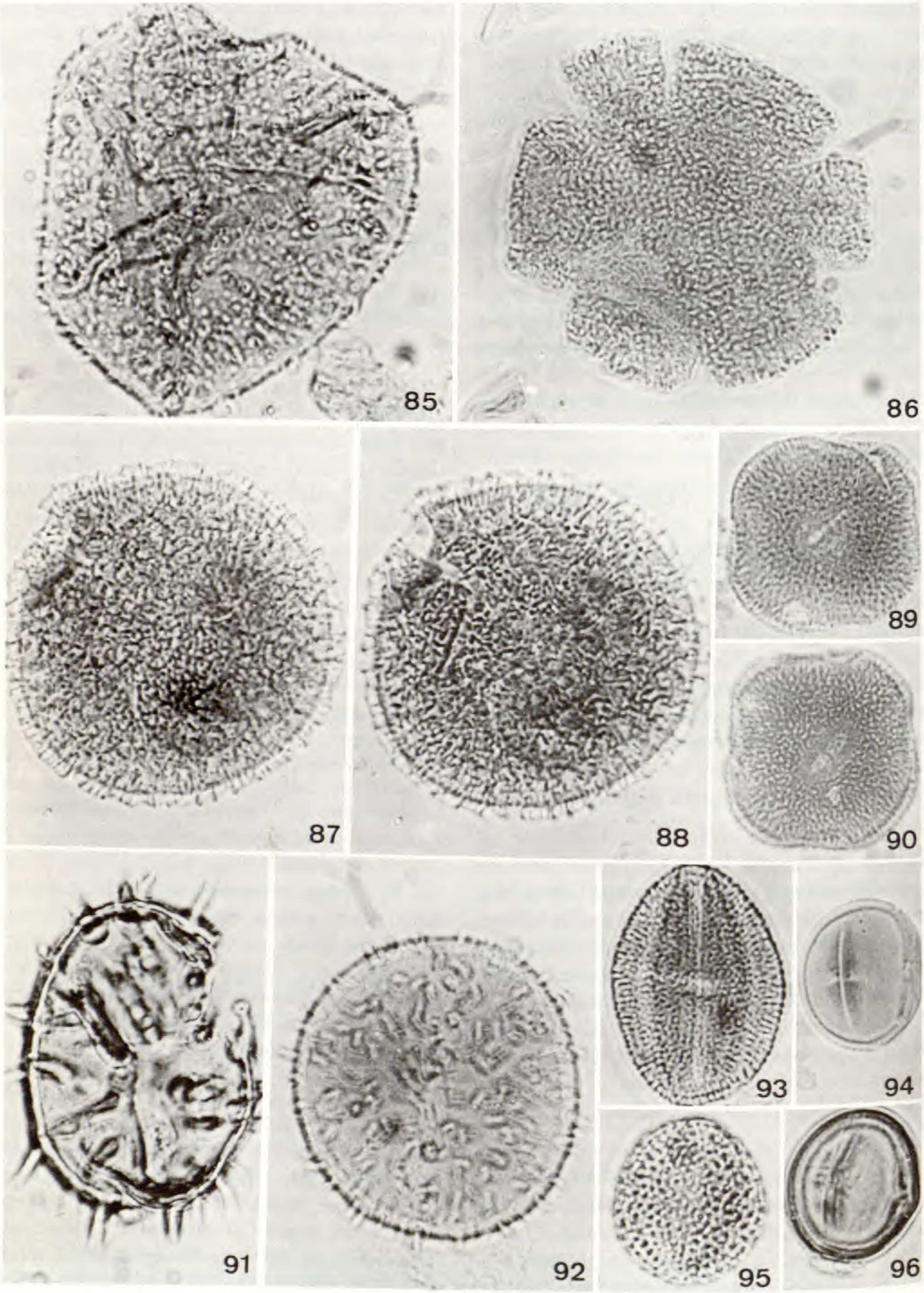
Unknown 20 (Figs. 89, 90). Oblate, amb square; apertures obscure, four(–six) colpi or colpi with pores, apertures equatorially arranged, meridionally elongated, equidistant, with two additional apertures possibly at each pole; finely reticulate, width of muri and diameter of lumina 1 μm or less; tectate-perforate, wall 3 μm, individual columellae evident in median section (400× magnification); 35 μm.

This specimen may be an aberrant form. There appear to be four colpi (with pores?) about the equator, and one at each pole. Grains with a similar number and arrangement of apertures were not encountered in the modern reference collection or in the literature examined.

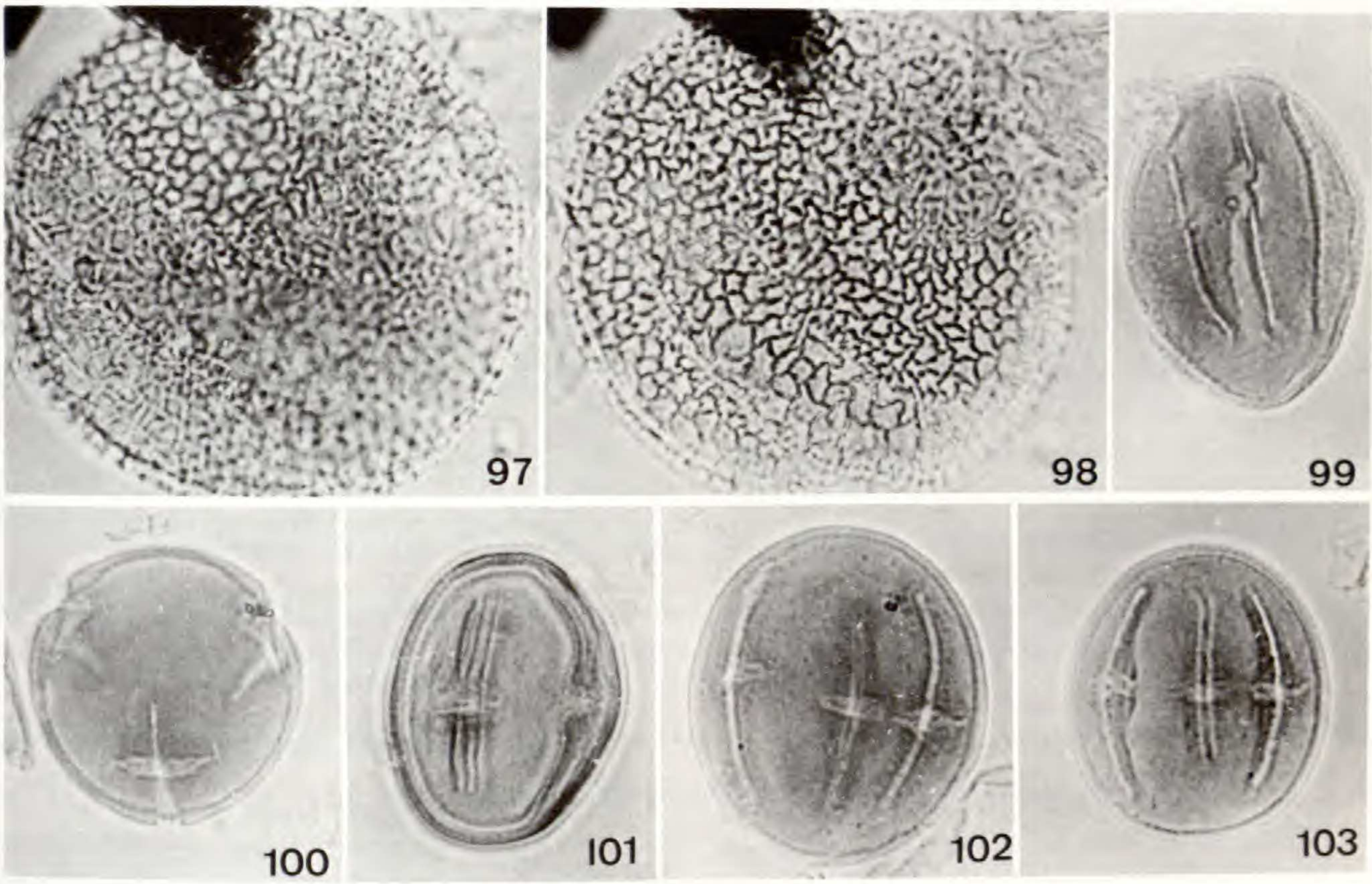
Unknown 21 (Fig. 95). Prolate to prolate-spheroidal; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 22–24 μm long, extending nearly entire length of grain, inner margin entire; reticulate, reticulum heavy (columellae ca. 2 μm thick), width of muri and diameter of lumina ca. 1 μm, lumina circular to polygonal; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 28 × 26 μm.

Unknown 22 (Fig. 94). Prolate to prolate-spheroidal; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, colpi straight, narrow, 18–20 μm long, inner margin entire, costae colpi 3–4 μm wide, broadening at pores, pores situated at midpoint of colpus, slitlike (1 × 4–5 μm); psilate to faintly scabrate; tectate, wall 3 μm thick, individual columellae just visible in median section (400× magnification); 27 × 23 μm.

Unknown 23 (Fig. 96). Prolate to prolate-spheroidal, tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, colpi



FIGURES 85–96. Fossil pollen from the Gatun Formation.—85. Unknown 14, SL-103, 253′, 15, ESF K-55.—86. Unknown 15, SL-103, 253′, 2, ESF R-36.—87, 88. Unknown 18, SL-103, 253′, 1, ESF G-49.—89, 90. Unknown 20, SL-103, 253′, 1, ESF L-35.—91. Unknown 17, SL-103, 253′, 7, ESF N-29.—92. Unknown 16, SL-103, 253′, 2, ESF T-41.—93. Unknown 24, SL-103, 253′, 13, ESF H-46.—94. Unknown 22, SL-103, 253′, 1, ESF F-36.—95. Unknown 21, SL-103, 253′, 1, ESF M-39.—96. Unknown 23, SL-103, 253′, 6, ESF H-37.



FIGURES 97–103. Fossil pollen from the Gatun Formation.—97, 98. Unknown 19, SL-103, 253′, 6, ESF G-32.—99. Unknown 27, SL-103, 253′, 2, ESF N-46.—100, 101. Unknown 25, SL-103, 253′, 1, ESF O-37; SL-103, 253′, 5, ESF K-45.—102, 103. Unknown 26. SL-103, 253′, 12, ESF P-22; SL-103, 253′, 13, ESF O-51.

straight, narrow, 22–24 μm, extending nearly entire length of grain, inner margin entire, costae colpi 3–4 μm wide, pore situated at midpoint of colpus, slitlike (1 × 4–5 μm); psilate; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 26 × 23 μm.

Unknowns 22 and 23 may represent variations of the same pollen type. The former has costae colpi that broaden at the pores, while the latter is more psilate and the wall more homogeneous.

Unknown 24 (Fig. 93). Prolate; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 24 μm long, extending nearly entire length of grain, costae colpi 4–5 μm wide (obscure), pore situated at midpoint of colpus, elongated equatorially, 3 × 5 μm; finely reticulate, width of muri and diameter of lumina ca. 1 μm; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 45 × 30 μm.

These grains are similar to those of certain Anacardiaceae and Euphorbiaceae, but an exact match could not be found. They are frequent in low percentages in Gulf/Caribbean Tertiary deposits, and have been reported from the Gatuncillo, La Boca, and Paraje Solo formations.

Unknown 25 (Figs. 100, 101). Prolate; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 20–22 μm long, inner colpus margin entire, costae colpi 3–4 μm wide, thicker at pore (4–5 μm), pores situated at midpoint of colpus, slitlike (1–2 × 4–6 μm); psilate to scabrate; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 37–44 × 24–28 μm.

These specimens may include some tetracolporate forms and are similar to several Sapotaceae, including *Caesaria*, a pantropical genus of about 250 species. Eight were recognized for Panama by Robyns (1968), and D'Arcy (1987) listed 17 species. Most grow in moist habitats, but some range into drier premontane or tropical dry forests. Pollen of *Caesaria* includes both tricolporate and tetracolporate forms. It has been reported from the Gatuncillo, San Sebastian, Culebra, and Paraje Solo formations.

Unknown 26 (Figs. 102, 103). Prolate to prolate-spheroidal; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 21–24 μm, inner margin entire, costae colpi 3 μm wide, thicker at pores (4 μm), pores situated at midpoint of colpus, slitlike (1–2 × 3–

5 μm); psilate to scabrate; tectate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 36–41 × 33–38 μm.

Unknowns 25 and 26 are similar and may represent variations of the same pollen type. The former has slightly thicker walls and costae colpi.

Unknown 27 (Fig. 99). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 28–30 μm long, inner colpus margin minutely dentate; scabrate; tectate, wall 2 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 42 × 30 μm.

The specimen may represent a *Quercus* grain that is slightly corroded, hence the granular appearance of the colpus margin.

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